

AUTOGAMY AS A FERTILITY ASSURANCE STRATEGY
FOR FORBS IN THE TALLGRASS PRAIRIE

by

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INTRODUCTION - ADVANTAGES OF SEXUAL REPRODUCTION

Sexual reproduction must involve some selective advantage to counteract the "meiotic cost" (Maynard Smith 1970, Williams 1975, Williams and Mitton 1973) of contributing fewer genes to the next generation when compared to the parental fitness of organisms reproducing by asexual means. For angiosperms, the loss of efficiency in seed set as well as energetic costs involved in the loss of pollen not reaching a receptive stigma and in producing structures to attract and reward animal agents (Solbrig 1976) also forces the question, why is sexual reproduction advantageous?

Solbrig (1976) outlines the advantages of sexual reproduction in plants as (1) the production of new individuals possessing parental genes that can be dispersed and go dormant, and (2) the formation of new recombinant genotypes. Population geneticists overwhelmingly support the hypothesis that the primary function of sexual reproduction is to maintain and increase genetic diversity. One camp of thought maintains that it is at the population level that this storehouse of genetic recombination is beneficial and that populations with greater genetic variability evolve more rapidly than do asexual populations, and therefore are better able to survive environmental changes (Fisher 1930, Muller 1932, Darlington 1939). Many early authors accepted this "classical hypothesis" (as enumerated by Solbrig (1976), p. 263). Texts were written (Faegri and van der Pijl 1966), as well as commentaries (Whitehouse 1959), which accepted group selection as the profound force for the evolution of sex.

More recent authors have championed the short-term advantages of

sex (Ghiselin 1974, Maynard Smith 1971, 1976, and for the most part in 1978, Solbrig 1976, Treisman 1976, William 1975, Williams and Mitton 1973). They have concluded that the immediate fitness (in terms of meiotic or energetic cost) of the individual is not necessarily sacrificed for the long range flexibility of the population. Likewise, they believe that the individual's "Darwinian fitness" associated with the production of genetically variable offspring has indeed been the selective force for the evolution of sex.

WHY INBREEDING

Inbreeding, although a sexual process, theoretically produces a smaller variety of recombinant genotypes for an individual or a population than allogamous breeding. The disadvantages of inbreeding were also emphasized by early developments in the genetics of hybrid vigor and theory of inbreeding (Jain 1976). Darwin's (1877) early experiments showed that self-fertilization was injurious in terms of height, weight and fertility of progeny. Later authors have added data in support of inbreeding depression (Lloyd 1965, Coles and Fowler 1976, Solbrig and Rollins 1977). Furthermore, the selective advantages of outcrossing have been widely acclaimed (Levin 1975, Solbrig 1976).

Maynard Smith (1978) stated that if a species were entirely selfing, the species would suffer the same long-term disadvantages as a parthenogenetic population but that there is a big difference in long-term evolutionary results between 100% and 99% selfing in a population. Apparently some selfing species consist of a number of biotypes of differing genetic make-up (Stone 1957, Allard 1965, Kannenberg et al. 1967, Allard et al. 1968). Many findings have shown that most self-

compatible species probably outcross with unrelated or distantly related individuals at least occasionally (Allard 1965, Jain and Marshall 1967, Kannenberg et al. 1967, Allard et al. 1968, Jain 1969, Solbrig and Rollins 1977) to form the progenitors of these new biotypes. Also, Stebbins (1950) proposed that as a compensatory mechanism for the genic homozygosity in inbreeders, high chromosome numbers or chiasmata frequency (now termed recombination index) would be more likely. Lokki (1976) provides a model in support of this idea that the functional heterozygosity and buffering affects against mutation are increased with polyploidy. Gibbs et al. (1975) provided evidence that with increasing amounts of selfing in five species of Senecio, the recombination indices increased accordingly. Arroyo (1973) also provides evidence in Limnanthes.

Theories on the adaptive advantages of inbreeding have been numerous in recent years because the focus on 'genetic systems in inbreeders has been integrated with ecological, genetic, and karyotypic studies and viewed in an evolutionary context. Jain (1976 p. 475 Table 1) provides a literature review and a categorization of hypotheses on the evolution of inbreeding. Hypotheses of narrow applicability will not be included in the following discussion.

Early 19th century naturalists observed that self-fertile species were more common at high altitudes and latitudes in Europe and had devices to ensure self-pollination if cross pollination failed (Darwin 1876, 1877, Muller 1883, Henslow 1888). This was the beginning of evidence for and hypothetical thinking about the evolution of inbreeding as a fertility assurance mechanism.

Another main group of authors have considered the supposed "post-

fertilization advantages" of inbreeding. They concluded that selfing is not merely an escape from reproductive failure but it also is an adaptive strategy in systems favoring close local adaptation (Darlington 1939, Mather 1940, 1943, 1953). These authors maintain that short-term fitness, achieved by the phenotypic uniformity mitigated by the suppression of genetic variation, is obtained at the expense of decreased long-term flexibility in changing environments.

Several authors have argued against this genetic hypothesis for the evolution of inbreeding. They maintain that the fertility assurance mechanisms of inbreeding is far more important than positive selection pressure for decreasing the level of variability (Lloyd 1965, Arroyo 1973, Gibbs et al. 1975). The latter two papers cited evidence that, due to changes in the recombination index, heterozygosity actually increases with increasing levels of autogamy in a population.

However, the postzygotic explanation for the evolution of autogamy has found support in the literature (Stone 1957, Mosquin 1966) and seems to be an especially useful explanation when synthesized with various ecological considerations. Stebbins' (1950, 1957) models combine both the reproductive assurance provided by inbreeding which allows rapid establishment after long distance dispersal, perhaps by a single propagule ("Baker's rule", Baker 1955), and the idea that autogamy is good for maintenance of individuals with particular adaptive gene combinations after colonialization. Pioneer associations and temporal habitats with great fluctuations in climate are typical in colonization. Data on 201 species of the tribe Cichorieae lend support to this hypothesis of self-fertilization being important in unstable habitats (Stebbins 1958). Other authors have pointed to inbreeding having

selective advantage in colonizing species, too (Allard 1965, Grant 1975). Empirical evidence has been provided in the Phlox family (Grant and Grant 1965), Mirabilis (Cruden 1973), and with entire communities found in habitats characterized by disturbance regardless of the available pollinators (Moldenke 1976).

The preponderance of thinking and evidence today coincides with that of the early naturalists - inbreeding has evolved mainly as a reproductive assurance mechanism where conditions exist to limit cross-pollination either by energetic costs to the plant or factors that influence the activity, abundance, or effectiveness of the pollen vectors (Fryxell 1957, Faegri and van der Pijl 1966). Observations of increased autogamy with latitude (Kevin 1972), altitude (Clausen and Hiesey 1960) and time-of-season (Cruden 1973) have sparked many speculations based primarily on correlations between autogamy and one-to-many factors affecting fertility assurance.

Selfing has been proposed as an adaptive strategy for fertility assurance where fluctuating climate between seasons (Stebbins 1950, 1957, Moore and Lewis 1965) or long distance dispersal (Baker 1955) has caused population reductions which can make effective cross-pollination more difficult. These are situations where high seed set would be at a premium and genes promoting selfing would be at an advantage for rapid establishment and perpetuation of an individual's progeny. Correlative evidence exists for this hypothesis (Ornduff 1966, Lloyd 1974). Population reductions due to external environmental stresses within a species' normal range has also been linked to increases in obligate selfing (Levin 1972b).

Autogamy has been theorized to be important where energetic costs

to the plant, such as the production of showy chasmogamous flowers, nectar, and abundant seed, are difficult to meet. Such conditions might exist where ambient temperatures are low, such as in the Arctic (Heinrich and Raven 1972, Kevin 1972), where light is limited for photosynthesis (Schemske 1978), during periodic droughts (Stebbins 1957, Bradshaw 1965), and in seasons or places where plants are under high herbivore loads (Schemske 1978). Much of the focus for autogamy correlated with late spring flowering in woodlands has been based on energetic considerations for the plant.

Data for alteration of breeding systems in response to poor chances of cross-pollination because of abiotic factors affecting pollinators is abundant. Climatic severity and unpredictability and the subsequent lack of success for pollen vectors has been charged as the reason for less obligate outcrossing with increasing altitude (Moldenke 1975, 1976), grassland and chaparral communities periodically ravaged by fire (Moldenke 1976), and in those species flowering in the changeable spring weather of Mediterranean climate (Stebbins 1957, Kannenberg and Allard 1967). Depauperate pollinator populations appropriate for species in foreign or colonized areas, or where proper pollinators have been exterminated, has been linked to high levels of self-pollination (Rick 1950, 1966, Faegri and van der Pijl 1966). Adverse conditions for cross pollination such as drought (Stebbins 1970, Arroyo 1973) and excessive moisture (Hagerup 1950, 1951, Stebbins 1970) which reduce populations and activities of pollinators have also been linked to the origin and perpetuation of self-fertilization.

Poor chances for pollination within a season have presumably caused the evolution of autogamy due to lack of coincidence of flowering and

pollinator emergence (Solbrig and Rollins 1977), and less pollinator activity on flower populations that are small and bloom early due to their physiographic location (Lloyd 1965).

Competition for pollinators among sympatric plant species could be the selective pressure that shifts flowering time. Species losing out in such competition may find it advantageous to reduce their reliance upon pollinators and become more autogamous (Grant and Grant 1965, Levin 1972a, Levin and Anderson 1970). Levin (1972a), however, states that the paucity of pollinators as well as competition for pollinators must be proven before the hypothesis that competition promotes autogamy can become more than mere speculation.

Competition for pollinators by plants has been a common assumption in the literature. Competition between crop plants and one or more other species has been observed (Filmer 1941, Free 1968), but the majority of speculation has centered upon competition for pollinators in entire plant communities. Heithaus (1974) rightly asserts that experimental methods are impractical for determining competition for pollinators in large communities and indirect evidence must be used. It has been suggested that major support for this hypothesis can come from observing divergence of flowering times in plant communities (Mosquin 1971, Heinrich and Raven 1972, Heithaus 1974). Evidence for staggered blooming times in communities began with Robertson (1895, 1924) and has been supplemented by data from many plant communities (Hocking 1968, Mosquin 1971, Frankie et. al. 1973, Pojar 1974, Heinrich 1975a&b, Reader 1975, Stiles 1975). Assortment of blooming times in all of these studies was linked to the reduction of competition for pollinators for those plants flowering within the community. Temporal displacement of certain

plants which offered less floral reward than others has also provided indirect evidence (Mosquin 1971) that competition for pollinators exists. For many, competition for pollinators is an assumption leading to further thinking about community structure (Levin and Anderson 1970, Straw 1972). Likewise, predictions made and tested from the competition-for-pollinator hypothesis have added even more credence to this hypothesis (Heithaus 1974). Yet, the importance of interspecific competition in shaping community structure is still a controversial issue (see review in Schoener 1982).

Whether competition for pollinators operates in the tallgrass prairie is still purely speculative. The facts remain that not all pollinator-attracting plants flower at the same time and that at times when climate is adverse for cross-pollination, autogamy would be advantageous for fertility assurance since insect pollination is extremely important among grassland forbs (Baker and Hurd 1968).

This complex interaction between the plants (phenology and reproductive mode) and the pollinators (forager activity and reproductive bionomics) has much support in the literature concerning community structures (Macior 1971, Heithaus 1974). Phenology as an evolved character timed with pollinator probabilities influenced by weather factors has much correlative support in the literature (Jarzen 1967, Frankie et al. 1974, Gentry 1974, Schemske 1977, Schemske et al. 1978). In fact, it can be assumed that climatic factors are the proximate cues for plants to time themselves with good pollinator probabilities. Effects of climatic factors on phenology of plants has received much attention (Lindsey and Newman 1956, Lettau 1965, Vezina and Grandtner 1965, Jackson 1966, Croat 1969, Caprio et al. 1970, Vasek

and Sauer 1972, Taylor 1974, Halverson and Patten 1975, Reader 1975, Schemske 1978), as have the proximate factors influencing inbreeding (Harlan 1945, Schemske 1978 many references).

In summary, it has been hypothesized that within a community some species may find it advantageous to become less reliant upon outcrossing and shift more toward inbreeding as a fertility assurance mechanism during times when the probability for pollinator effectiveness is low. Competition for pollinators may be the driving force to shift flowering of some plants to less desirable times for pollination. This study will attempt to identify times within flowering seasons that are unfavorable for pollinator activity by analyzing climatic factors that effect pollinator activity. These times will then be correlated with increases in community reliance upon inbreeding for native, insect-attracting forbs of the tallgrass prairie region.

STUDY AREA

Konza Prairie Research Natural Area (KPRNA) is a 3487 hectare (8616 acres) sample of unplowed native prairie. It was acquired for ecological research and managed with the goal of approximating pre-settlement conditions. KPRNA is located approximately 39°04'N to 39°08'N latitude and 96°32'W to 96°37'W longitude in Riley and Geary counties in the Flint Hills of eastern Kansas. Field research for this study was undertaken on approximately 115 hectares south of the Riley-Geary county line on the eastern third of the area known as "old Konza".

The dominant species of the tallgrass prairie are four warm-season perennial grasses: big bluestem (Andropogon gerardii), little bluestem (Andropogon scoparius), Indian grass (Sorghastrum nutans), and switchgrass (Panicum virgatum). Forbs (angiosperms excluding trees and shrubs, cyperaceous and poaceous species, entirely aquatic species, and introduced species) are numerous throughout KPRNA. Approximately 300 of the 441 plant species are forbs according to Freeman and Hulbert (in press). Yet, forbs only contribute about 3% of biomass to the average species composition of the Flint Hills prairie (Weaver, 1954).

METHODS

Data for Plant Species

Census of species in flower. -- From April to October in 1979 and 1980, a list of forbs and woody shrubs that attract insects to its flowers was compiled every ten days. Care was taken to transect as many habitats and management areas as possible within the study site (see Figure 1). Roughly the same area was covered during each census. A representative of each plant at the advent of its flowering was collected and identified with the help of the Kansas State University (KSU) Herbarium. Nomenclature follows Freeman and Hulbert (in press).

Selection of species. -- Non-native species were first excluded from each census list. Then, the list of species gathered for each census was randomized using computer-generated random number tables. Beginning at the top of the randomized list, as many species as possible were treated during that 10-day census period. Species discovered flowering during the 10 days between censuses were added randomly to the list. Randomization and frequent censusing helped avoid a biased sample of species from the community.

Treatment of species. -- Within a population, individuals which had similar growth form, maturity, and reproductive vigor were chosen. Individuals were flagged and many inflorescences from each individual plant tagged for identification. The number of flowers and/or composite heads for each inflorescence were then counted. The term inflorescence applies here and after to a single flower (e.g., Ruellia humilis Nutt.), a cluster of flowers (e.g., Gaura parviflora Dougl.), a composite head

Figure 1. Map of Konza Prairie Research Natural
Area showing study site.

(e.g., Senecio plattensis Nutt.), a group of composite heads (e.g., Ambrosia artemisiifolia L.), or all flowers on a plant (e.g., Oxalis violacea L.). Data were collected and recorded in this way according to a subjective judgement on what would be an attracting unit for an insect for each plant species. A voucher specimen was collected for each species with the habitat noted.

For each species tested, one group composed of at least three individuals was protected from insect visitors while the control group, also with a minimum of three individuals, was left unprotected. Populations were checked regularly before disseminule dispersal. Inflorescence collections were dried in an oven for 24 hours to minimize herbivory of fruits and fungal damage before analysis.

Enclosures. -- Cages were constructed of 1.25mm nylon mesh supported by dowels. They provided a free-standing enclosure which excluded insect visitors but neither inhibited the natural wilting of a flower nor caused any unnatural physical disturbance to the corolla. Cages were made in three sizes to enable enclosing entire plants of different sizes. Drawstrings at the top and bottom of the cage allowed easy access to the plant and a complete barrier against insects. Very tall plants (e.g., Silphium speciosum Nutt.) had flower heads enclosed in wire cones covered by nylon mesh and supported by tall wooden dowels to minimize extra motion in the wind.

Phenology. -- Concurrent with the treatment of each species, individuals of the same species were tagged for phenological study. Phenological readings were taken every 1-3 days. Data collected included time of flower-bud maturation, length of flowering, time of

flower to fruit, and in some cases, time to dispersal. The initial day and final day of flowering were noted for the entire phenological group and an average-day-of-flowering was calculated. This mean was calculated from the set of median days-of-flowering for each inflorescence observed. These records were kept to give estimates of flowering dates and length-of-flowering for the species without handling individuals in the control and treatment groups. This helped avoid artificially increasing the probability of pollination.

Laboratory Analysis. -- For each inflorescence collected, the number of flowers and/or potential fruits produced was determined by one of several possible ways. In some cases, the original field count was used. Others were done by counting scars on the peduncle (e.g., Dalea candida Michx. ex Willd. var. candida, Verbena bipinnatifida Nutt.), or counting unfertilized flowers which persisted in the heads and adding these to the fruit count (e.g., Vernonia baldwini Torr. var. inferior (Small) Schubert). Also, some estimates were made by dissecting collections and getting an estimate for an average inflorescence. As an example of this method, Croton monanthogynas Michx. produces approximately 7.6 flowers per axil. Thus axils on the treatment and control inflorescences were counted and multiplied by this number to get an estimate of the number of flowers per inflorescence. Lastly, in rare cases, the largest number of fruits produced for an inflorescence within the sample had to be found and declared to be the potential number of fruits for each inflorescence (e.g., Rosa arkansana Porter var. suffulta (Greene) Cockerell). Only those flowers that could produce fruit by being perfect or pistillate were included.

Care was taken to exclude data where herbivory clouded either estimates for potential flowers or viable fruits. In some cases, entire species had to be thrown out of the data set because of herbivory to the control groups. After flowers from each inflorescence were counted, viable fruits were counted. A viable fruit was defined as one that was either filled with endosperm, as in the single seed of Dalea purpurea Vent. var. purpurea, or had any seeds at all in it, e.g., Physalis virginiana. If it was possible, counts were made of viable seeds per fruit as well. Potential seeds were usually counted as the largest number of seeds per fruit recorded for a species at a certain time, but for some species an actual number could sometimes be determined for each fruit (e.g., Callirhoe involucrata (T.&G.) A. Gray). Seed data was useful when certain species set the same amount of fruit in control and treatment but where actual fertilization was different.

Data was recorded as fruit per potential fruit and seeds per potential seeds for each inflorescence of an individual plant within a treatment. This type of data gathered for a plant species within a certain time period, within a certain year will here after be referred to as species unit data.

Weather Data

There is virtually no information concerning how weather factors affect pollinator activity in natural communities. A majority of the literature concerns honeybee activity in controlled environments or in agricultural settings such as orchards. Even though most insects enter torpor at more frequent intervals than this social Hymenoptera (Linsley 1958, Heinrich 1975), a majority of the information is helpful in determining which weather factors influence foraging behavior in wild bees (Linsley and MacSwain 1947). Some literature is also available for bumblebee activity (Bruggemann 1958, Hocking and Sharplin 1964, Heinrich 1972, 1974, 1975) but because of their large size, high metabolic rate, and dense pile, they are not typical representatives of pollinators on the tallgrass prairie even though they contribute to part of the pollination.

It should be noted that effects of weather factors on pollinator activity are influenced by differences in locality, age of pollinators (Free and Spencer-Booth 1958), strength of colony (Woodrow 1932, Brittain et.al. 1933), time of day (Lundie 1925, Brittain et.al. 1933), relative humidity (Miller 1951, Free and Spencer-Booth 1962), time of season (Lundie 1925, Uvarov 1931, Brittain et.al. 1933), cloud cover (Brittain et.al. 1933), and, of course, species (Heinrich 1974). Thus, categories within each weather factor have been left fairly broad.

Data for each weather factor was compiled for each day from April 29 to October 19 of 1979 and 1980. The range of possible values for each weather factor was divided into categories according to its effect on pollinator activity. Each category was given a corresponding

weighting factor. The following sections describe these categories for each weather variable and show the weighting factor in parenthesis. These weights ranged from +1 to -2. The number of hours that the weather measurement for that variable fell into a given category each day was then determined. This value was divided by the potential number of hours that it could have happened (usually the total number of daylight hours or 24 hours) and multiplied by the weighting factor. This weighted score was calculated for each category within each weather factor. The weighted weather score for each day, then, was the sum of all the weighted categorical values for that day. This weighted day score was thus considered to be a relative estimate of the day's suitability for pollinator activity. Differences in pollinator activity during the growing seasons of 1979 and 1980 were inferred from the differences in weather factors that more than likely affect this activity.

Temperature. -- Initiation of flight has been observed for honeybees as low as 5.6°C (Woodrow 1932). Other observers have reported flight initiation within the range of 8.9°C - 11.1°C (DeOng 1925, Marshall 1929, Vansell 1942). Other data show the range for flight initiation for honeybees as 15.6 - 18.3°C (Phillips 1927, MacDaniels and Heinricke 1929, Brittain et. al. 1933). However, observations on native species in natural habitats (Michener and Rettenmeyer 1956, Schenkske 1977, 1978) as well as honeybees (Thorp 1979) indicate 13°C is a minimum temperature for pollinator flight initiation.

Although honeybees have been observed to have good flight at 41°C (Jaycox 1976), most observers agree that above 26.7°C, activity begins

to decline (Park 1923, Lundie 1928, Brittain et.al. 1933, Linsley and MacSwain 1947, Willson and Price 1977, Reddy 1979) and that over 32.2°C, the decline is dramatic (Brittain et.al. 1933, Miller 1951, Free and Spencer-Booth 1962). All endothermic animals have a narrow range of maximum temperature for flight (Heinrich 1974). They will slow down or end foraging because they either can no longer dissipate heat (Heinrich 1972) or must switch to gathering water (Schaffer et.al. 1979).

Several studies show that an optimum temperature for pollinator activity is within the range of 18.3°C - 23.9°C (Lundie 1925, Phillips 1927, Brittain et.al. 1933, Miller 1950). Other investigations support this optimum temperature range by reporting that temperatures within this range did not have any detrimental effect on pollinator activity (Lee 1965, Hutson 1926).

In light of the above discussion, categories for temperatures were set at $\leq 13^{\circ}\text{C}$ (-1), $\geq 26.7^{\circ}\text{C}$ (-1), and $18.3^{\circ}\text{C} - 23.9^{\circ}\text{C}$ (+1). Hourly temperature readings, as well as cloud cover, relative humidity and rainfall, were taken at the no. 2 station, Call Hall, Kansas State University, Manhattan, Kansas. The potential number of hours was calculated as daylight hours between sunrise and sunset (CST) at Manhattan, Kansas (39°12' N.L., 96°35' W.L.).

Wind. -- Wind velocity is recognized as being one of the greatest limiting factors for flying insects (MacDaniels and Heinricke 1929). For honeybees as well as other small bees (Vansell 1942), winds greater than 20 - 25 mph will stop flight completely (Hutson 1926, Marshall 1929, Jaycox 1976). Some observers have stated that little progress is made even at 15 mph (Park 1923, Jaycox 1976, Thorp 1979). Some small

effects are seen on pollinator flights as winds increase to 10 - 11 mph (Lundie 1925, Brittain et.al. 1933, Lee 1965, Joyce and Hansen 1968, Reddy 1979).

Categories for wind velocities were thus set at < 10 mph (9 knots) (+1), 9 knots - 16 knots (-1/2), and > 20 mph (17 knots) (-1). Windspeed was taken 10 minutes before each hour at the City of Manhattan Airport, Manhattan, Kansas and potential hours were the total number of daylight hours.

Cloud Cover. -- Honeybees (Lundie 1925, Butler and Finney 1942, Vansell 1942), other bees except bumblebees (Brittain et.al. 1933, Linsley 1958, Cruden 1972, Estes 1976), flies (Joyce and Hanson 1968) and some pollination systems (Beattie 1971) show strong cessation of activity with the occlusion of the sun. In one study, though, there seemed to be a strong relationship in the tallgrass prairie between potential pollinator activity and increasing cloud cover (Gerould et.al. unpublished). In my study, cloud cover was measured as the number of daylight hours where half or more of the maximum light for that time of year was obscured for at least one half of the hour. Potential hours were total daylight hours. Because of the conflicting information concerning cloud cover and pollinator activity, cloud cover ratios were not given a weighted value nor added into the daytime weighted scores.

Relative Humidity. -- Some investigators have found that relative humidity has very little direct influence on pollinator activity (Hutson 1926, Brittain et.al. 1933). Yet, others have established that pollinator activity is influenced by nectar concentration and abundance (Butler 1945, Weaver 1957, 1965) which in turn are largely influenced by

the relative humidity and the presence or absence of dew or rain (Hutson 1926, Scullen 1940, Butler 1945, Nye and Pederson 1962, Hocking 1968). Nectar is generally produced in dry (but not too dry), warm weather (Faegri and van der Pijl 1966). Low relative humidity and hot weather have been shown to depress pollinator activity (Uvarov 1931, Free and Spencer-Booth 1962, Reddy 1979) and Linsley and MacSwain (1947) have shown that below 30% relative humidity insect activity dips. Very high relative humidities also seem harmful to honeybees (Wolfenbarger 1934, Woodrow 1935) and dew might have the same effect on insect activity as rain does: smaller insects might be handicapped by droplet surface tension, nectar is more dilute, and water on anthers prevents anther dehiscence (Gerould, unpublished).

Since the dew point is approximately 90% relative humidity, categories important to pollinator activity were determined to be $\geq 90\%$ in daylight hours (-1) (the hours that dew would affect pollinating) and $< 30\%$ in 24 hours (-1) (the hours that affect nectar concentration and abundance). One minus the addition of the latter two humidity percentages was given a weighted score of +1.

Rainfall. -- Willson (1977) found no correlation between rainfall and pollinator activity but other investigators have found that rain causes complete cessation of pollinator activity (DeOng 1925, Hutson 1926, Lee 1965, Thorp 1979) unless the pollinator is a bumblebee (Uvarov 1931). Thus it was determined that important categories for rainfall were the number of hours in which there was any rainfall at all (-1) and 1 minus this percentage (+1). Potential hours were total daylight hours.

Choosing time periods. -- Weighted day scores for weather were plotted for the growing seasons of 1979 and 1980. To discern time periods where differences in pollinator activity had likely occurred, weighted day scores were grouped together according to how the scores changed throughout the growing season. Thus, a cluster of scores was considered to be a time period where pollinator activity would predictably be different from the next. Ten time periods over the two growing seasons were identified (see Figures 2 and 3).

Weather scores for time periods. -- A weather score was calculated for each species unit by averaging the weighted weather scores of all the days in which the species' flowers were open for pollination as determined from the phenological records. This score (weather^{species}) best represented the weather that affected pollinator activity for each plant species treated at a given time.

Plant species units were grouped into time periods according to their average day of flowering. The weather score for a time period (weather-time^{species}) was calculated by averaging all the weather scores (weather^{species}) for those species grouped into that time period. This time period weather score did not necessarily represent the weather of that time period but the weather that directly affected the species within that time period. Thus, some weighted day scores were not used, while some were used extensively. Some day scores even came from other time periods if the species continued to flower past a time period boundary. All species had equal weight in determining the weather scores for a time period. It could be expected that weather-time^{species} data would correlate negatively with autogamy data for plant species if

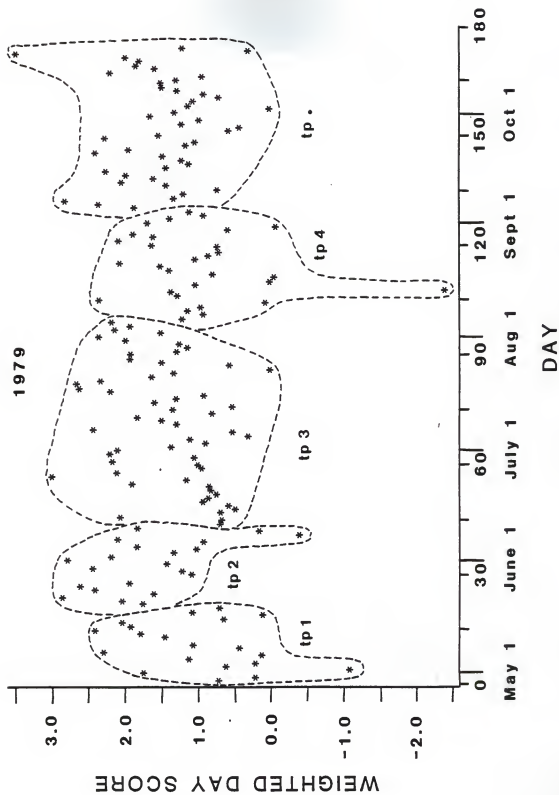


Figure 2. Weighted day scores for weather during
1979 clustered into time periods. Day 1
is April 29. tp = time period.

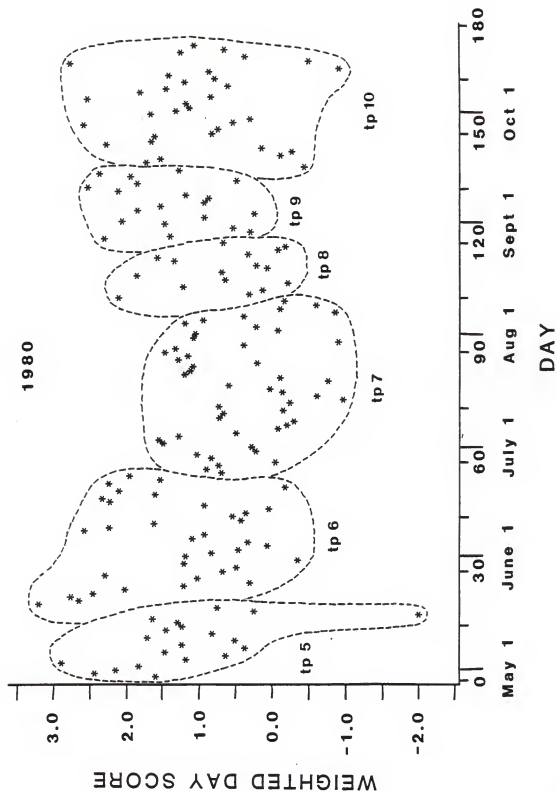


Figure 3. Weighted day scores for weather during 1980 clustered into time periods. Day 1 is April 29. tp = time period.

the plants were showing a strong facultative ecological response to weather that affects pollinators.

A second weather score for a time period was obtained by averaging all weighted day scores in the period (weather-time^{average}) (Figure 4). Presumably this weather index would more accurately represent weather variables that generally affected the species unit and is the best representative of weather for a certain time of year. Autogamy data for plant species should correlate negatively with weather-time^{average} if the forb breeding strategies are adapted evolutionarily to long-term weather patterns that affect pollinators. A summary of the weather scores are presented in Table 1.

Data Analysis

Plant species. -- A separate statistical analysis was carried out for each plant species unit to discern differences between control (C) and treatment (B) groups. Fruit per potential fruit or seed per potential seed data were used to generate % fertilization B and % fertilization C. Fruit data was generally used in the subsequent analysis unless seed data showed a difference between B and C groups where fruit data did not, or where the difference was even greater than the fruit data.

The design of the experiment and subsequent data collection corresponded to a 1-way treatment structure with subsampling. The plant species units comprise the experimental units for testing treatment effects, and the inflorescences within a plant comprise the experimental units for testing for differences between plants within a species and

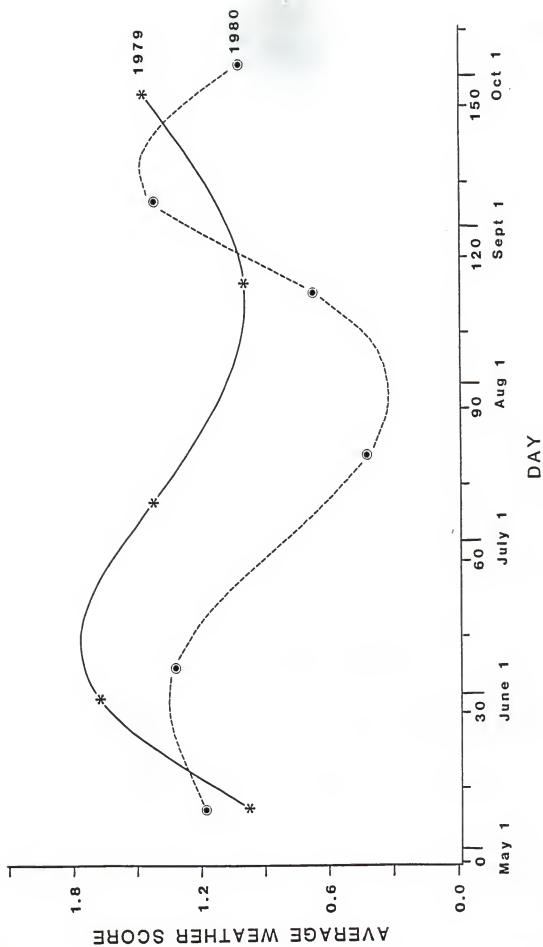


Figure 4. A plot of the average weighted day score (weather-time^{average}) for time periods in 1979 and 1980. These day scores are an estimate of the suitability of the weather for pollinator activity. Day 1 is April 29.

Table 1. Summary of weather indices within time periods.

<u>Time Period</u>	<u>Days ¹</u>	<u>Weather-time species</u>				<u>Weather-time averaged</u>			
		<u>N</u>	<u>Mean</u>	<u>Minimum</u>	<u>Maximum</u>	<u>N</u>	<u>Mean</u>	<u>Minimum</u>	<u>Maximum</u>
	1	1-21	--	--	--	20	.98	-1.07	2.39
	2	22-43	5	1.13	.89	21	1.67	-.39	2.86
1979	3	44-99	22	1.25	.72	56	1.42	.02	3.00
	4	100-129	7	1.30	1.07	30	.99	-2.38	2.36
	.	130-174	--	--	--	45	1.47	.03	3.50
<hr/>									
	5	1-20	--	--	--	20	1.17	-1.99	2.89
	6	21-56	7	1.25	.88	36	1.32	-.34	3.21
	7	57-104	13	.61	.33	48	.42	-.97	1.56
1980	8	105-120	10	.68	.44	16	.67	-.22	2.11
	9	121-140	6	1.46	1.13	20	1.42	.25	2.53
	10	141-174	7	1.25	1.01	34	1.02	-.91	2.77

¹Day 1 = April 29

treatment. The F-test from the ANOVA should be considered an approximation because the sample sizes were highly discrepant from plant species unit to plant species unit. For some species units, the degrees of freedom (df) for plant was 0 (only 1 plant in each treatment) or df for error was 0 (no variance within a plant and all the inflorescences were the same). In the second case, a 1-way ANOVA was used with the experimental units being individual plants. In the first case, a 1-way ANOVA was also used with the experimental units being the inflorescences within each plant. In the first case, the plant effects are unavoidably confounded with the treatment effects. These cases are indicated in Table 2 with a '1' superscript on the F value. Analysis was done with the Statistical Analysis System (SAS).

Using the F statistic in making comparisons between species is deceiving since df vary from treated species to treated species and thus the F is not measured on the same scale. To correct for this, a 1-tail area probability was calculated to the left of F, i.e., probability of observing an $F \leq$ the value when the null hypothesis was true.

For some species units, there was no variation between plants within a treatment. The ANOVA F is undefined in this case (i.e., $F = MSTRT / MSE = 0$). In these cases, a nonparametric test (Wilcoxin's Rank Sum Test) was used to compare the treatments. Wilcoxin's Rank Sum Test is still defined under these conditions.

A Chi-square (X^2) statistic was obtained for each set of data as well. An F statistic assumes data is from a normal distribution. For some plant species, the number of flowers observed for each inflorescence was small or the ratios for inflorescence data seemed bunched (i.e., either all 0 or 1). In these cases, a normal

Table 2. Summary of accumulated data and analysis between control and treatment groups for plant species.

Species	Year	Day Average	Fruit or Seed	χ^2	$\Pr\{\chi^2$	F value	V_1	V_2	$\Pr\{F$	Treatment (B)		Control (C)	
										actual fertil- potential	ization	actual fertil- potential	ization
<i>Achillea millefolium</i>	79	58	F	3.09	.92	.51 ^W	1	4.05	.49	$\frac{1045}{1507}$.69	$\frac{600}{824}$.72
<i>Asclepias viridis</i>	80	44	F ^A	2.18 ^W	.86	3.94 ¹	1	4.00	.88	$\frac{0}{74}$.00	$\frac{2}{69}$.03
<i>Allium stellatum</i>	80	151	F	19.52	1.00	1.81 ^{1W}	1	5.00	.76	$\frac{2^B}{86}$.02	$\frac{47}{196}$.24
<i>Ambrosia artemisiifolia</i>	80	135	F ^C	1.03 ^W	.69	.00	1	.95	.00	$\frac{20}{26}$.77	$\frac{18}{28}$.64
<i>Amorpha canescens</i>	79	62	F	914.65	1.00	14.19 ^{1W}	1	4.00	.98	$\frac{210}{4411}$.05	$\frac{1387}{4868}$.28
<i>Aster ericoides</i>	80	156	F	818.13	1.00	47.46 ^W	1	3.99	1.00	$\frac{8}{1307}$.01	$\frac{683}{1410}$.48
<i>Baptisia bracteata</i>	80	41	F ^D	7.06 ^W	.99	3.93 ¹	1	4.00	.88	$\frac{0}{7}$.00	$\frac{10}{17}$.59
													.96
													.00
													.10
													.17
													.01
													.00

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	$\Pr \chi^2$	F value	V_1	V_2	$\Pr < F$	Treatment (B)		Control (C)	
										actual potential	Percent fertil- ization	actual potential	Percent fertil- ization
Cacalia plantaginea	79	67	F	69.94 ^W	1.00	75.50	1	4.05	1.00	0 150	.00	55 145 ^E	.38
	80	64	F	19.87 ^W	1.00	3.30	1	3.00	.83	1 343	.00	18 277	.06
Callirhoe altceoides	80	55	F ^F	2.67 ^W	.90				.90 ^W	0 4	.00	2 4	.50
Callirhoe involucrata	79	50	F	7.77	.99	10.25 ^{1W}	1	1.00	.81	3 26	.12	6 11	.55
	79	50	S*	96.41 ^W	1.00	12.93	1	1.01	.83	21 385	.05	63 164	.38
	79	76	F	.90	.66	.54 ^{1W}	1	4.00	.50	2 31	.06	4 29	.14
	79	76	S*	24.01 ^W	1.00	1.33	1	4.29	.69	23 589	.04	64 551	.12
Cirsium altissimum	80	126	F	24.76	1.00	.71 ^W	1	4.08	.55	267 612	.44	460 1432	1.36
	80	144	F	.41	.48	.28 ^W	1	4.38	.38	15 544	.03	39 1167	.03
	80	156	F	39.87	1.00	.57 ^W	1	2.99	.49	0 397	.00	62 656	.09

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	$\Pr\{\chi^2$	F value	V_1	V_2	$\Pr\{F$	Treatment (B)		Control (C)	
										actual fertil- potential	Percent fertil- ization	actual fertil- potential	Percent fertil- ization
Croton capitatus	79	120	F* ^C	.01 ^W	.08	.03	1	5.48	.13	$\frac{10}{24}$.42	$\frac{6}{15}$.40
	79	120	S	.05 ^W	.18	.46	1	4.58	.47	$\frac{24}{27}$.89	$\frac{13}{15}$.87
	80	98	F* ^C	.03 ^W	.14	.33	1	1.00	.33	$\frac{4}{6}$.67	$\frac{5}{8}$.63
	80	125	F* ^C	.00 ^W	.00	.02 ¹	1	4.00	.11	$\frac{12}{13}$.92	$\frac{11}{12}$.92
Croton monanthogynous	79	99	F*	.00	.00	.04 ^{1W}	1	2.00	.14	$\frac{8}{88}$.09	$\frac{39}{432}$.09
	79	99	S	.37	.46	.46 ^{1W}	1	2.00	.43	$\frac{4}{8}$.50	$\frac{15}{39}$.38
	80	102	F*	.00	.00	.00 ^{1W}	1	2.00	.00	$\frac{237}{1616}$.15	$\frac{114}{776}$.15
	80	98	F ^G	21.00	.68	.45 ^W	1	5.22	.47	$\frac{372}{849}$.44	$\frac{149}{480}$.31
Desmanthus illinoensis	80	98	S*	79.98 ^W	1.00					$\frac{227}{1384}$.16	$\frac{186}{528}$.35
Erigeron annuus	79	41	F	3291.96	1.00	32.59 ^W	1	4.12	1.00	$\frac{83}{7071}$.01	$\frac{734}{1492}$.49

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	$\text{Pr}\chi^2$	F value	V_1	V_2	Pr<F	Treatment (B)		Control (C)	
										Percent actual fertil- potential ization	Percent actual fertil- potential ization	% B % C	
Erigeron strigosus	80	39	F	51.27	1.00	.20 ^W	1	4.16	.32	$\frac{1073}{1995}$	$\frac{1995}{3125}$.64	.84
Euphorbia marginata	79	108	F	2.12	.85	.95 ^{1W}	1	1.00	.49	$\frac{9}{18}$	$\frac{85}{126}$.67	.74
	79	108	S*	77.55 ^W	1.00					$\frac{6}{12}$	$\frac{205}{207}$.99	.50
Gaura parviflora	79	126	F ^H	8.00	1.00	1.15 ^W	1	4.11	.66	$\frac{152}{302}$	$\frac{97}{253}$.38	1.31
	80	92	F ^H	106.28	1.00	11.54 ^W	1	.76	.76	$\frac{179}{211}$	$\frac{51}{158}$.32	2.63
Hieracium longipilum	79	92	F	3.24	.93	.91 ^W	1	4.78	.61	$\frac{1106}{1365}$	$\frac{1605}{2045}$.78	1.03
	80	113	F	5.96	.99	.17 ^W	1	3.01	.29	$\frac{433}{484}$	$\frac{520}{616}$.84	1.06
	80	131	F	.83	.64	.06 ^W	1	2.22	.17	$\frac{514}{538}$	$\frac{621}{658}$.94	1.01
Hedyotis nigricans	80	94	F	19.41 ^W	1.00	45.42	1	3.94	1.00	$\frac{0}{41}$	$\frac{15}{39}$.38	.00
	80	113	F	1.77 ^W	.82	1.24	1	2.55	.64	$\frac{0}{17}$	$\frac{1}{10}$.10	.00

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	$\Pr\{\chi^2$	F value	V_1	V_2	$\Pr\{F$	Treatment (B)		Control (C)		% B % C
										actual potential	fertil- ization	actual potential	fertil- ization	
Hymenopappus scabiosaeus	80	40	F	192.14 ^W	1.00	38.25	1	2.91	.99	0 244	.00	192 358	.54	.00
Kuhnia eupatorioides	80	118	F	150.86 ^W	1.00	3.22	1	4.07	.85	3 619	.00	55 221	.25	.02
	80	135	F	268.20 ^W	1.00	70.41	1	4.06	1.00	0 303	.00	264 457	.58	.00
Lactuca ludoviciana	80	90	F	2.62	.89	.63 ^W	1	13.88	.56	548 559	.98	364 378	.96	1.02
	80	112	F	22.92	1.00	2.44 ^W	1	4.65	.82	335 370	.91	450 459	.98	.92
Lespedeza violacea	79	125	F	4.00 ^W	.95	1.59	1	2.23	.68	11 42	.26	4 6	.67	.39
	79	125	S*	1.93 ^W	.84	1.07	1	2.00	.59	0 7	.00	1 4	.25	.00
Linum sulcatum	79	75	F						.00 ^W	83 83	1.00	60 60	1.00	1.00
	79	75	S*	11.17 ^W	1.00	6.95	1	6.48	.96	728 829	.88	487 598	.81	1.08

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	$\text{Pr} \chi^2$	F value	V_1	V_2	Pr F	Treatment (B)		Control (C)	
										actual potential	Percent fertil- ization	actual potential	Percent fertil- ization
Lythrum alatum	79	75	F*	3.03	.92	1.00 ^{1P}	1	4.00	.63	$\frac{0}{68}$.00	$\frac{4}{92}$.04
	80	64	F	39.34 ^W	1.00	22.99	1	4.88	.99	$\frac{6}{101}$.06	$\frac{37}{81}$.46
	80	64	S*	242.42 ^W	1.00	6.45	1	18.48	.98	$\frac{7}{415}$.02	$\frac{635}{1494}$.43
Oenothera macrocarpa	79	46	F	2.43	.88	2.74 ^{1P}	1	4.00	.83	$\frac{0}{14}$.00	$\frac{3}{19}$.16
	79	77	F ^H	1.08	.70	.46 ^{1P}	1	4.00	.47	$\frac{33}{39}$.85	$\frac{27}{36}$.75
Calylophus serrulatus	79	77	S*	4.98	.97	.00 ^W	1	4.76	.00	$\frac{732}{2379}$.31	$\frac{401}{1464}$.27
	79	50	F							$\frac{5}{5}$	1.00	$\frac{4}{4}$	1.00
Opuntia macrohiza	79	50	S*	.52	.53	.03 ^{1P}	1	7.00	.13	$\frac{94}{210}$.45	$\frac{69}{168}$.41
	79	40	F	24.81 ^W	1.00	22.27 ¹	1	10.00	1.00	$\frac{0}{17}$.00	$\frac{13}{15}$.87
Dalea candida	79	73	F	38.89	1.00	1.76 ^W	1	4.00	.74	$\frac{69}{748}$.09	$\frac{156}{753}$.21

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	$\text{Pr}\chi^2$	F value	V_1	V_2	$\text{Pr}(F)$	Treatment (B)		Control (C)	
										Percent actual fertil- potential ization	Percent actual fertil- potential ization	Percent actual fertil- potential ization	% B % C
<i>Dalea purpurea</i>	80	66	F	136.17	1.00	55.86 ^W	1	4.00	1.00	$\frac{49}{851}$	$\frac{192}{704}$.27	.21
<i>Physalis virginiana</i>	79	52	F*	13.42 ^W	1.00	3.99 ¹	1	4.00	.88	$\frac{0}{18}$	$\frac{13}{25}$.52	.00
	79	108	F	5.93 ^W	.99	.92 ¹	1	4.00	.61	$\frac{9}{40}$	$\frac{19}{39}$.49	.46
	79	108	S*	24.83 ^W	1.00	1.10	1	2.90	.63	$\frac{0}{98}$	$\frac{25}{112}$.22	.00
	80	70	F*	1.85 ^W	.83	1.80 ¹	1	3.00	.73	$\frac{0}{16}$	$\frac{1}{9}$.11	.00
<i>Polygala verticillata</i>	80	108	F	1.07 ^W	.70	1.19	1	2.91	.64	$\frac{19}{81}$	$\frac{10}{61}$.16	1.43
	80	108	S*							$\frac{0}{14}$	$\frac{1}{42}$.02	.00
	79	79	F	4.46	.97	1.49 ^W	1	5.95	.73	$\frac{39}{78}$	$\frac{52}{78}$.67	.75
	79	79	S*	1.18 ^W	.72					$\frac{23}{40}$	$\frac{29}{42}$.69	.83
	79	105	F	1.65	.80	.82 ^W	1	1.00	.47	$\frac{39}{54}$	$\frac{67}{108}$.62	1.16
	79	105	S*	.15 ^W	.30					$\frac{108}{176}$	$\frac{36}{56}$.64	.95

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	Pr< χ^2	F value	V_1	V_2	Pr<F	Treatment (B)		Control (C)	
										actual fertil- ization	Percent fertil- ization	actual fertil- ization	Percent fertil- ization
Rorippa sinuata	80	49	F	1.58 ^W	.79	1.16	1	4.28	.66	$\frac{36}{54}$.67	$\frac{25}{46}$.54
	80	49	S*	33.46 ^W	1.00	15.91	1	4.98	.99	$\frac{4}{324}$.01	$\frac{30}{225}$.13
Rosa arkansana	79	40	F	1134.50 ^W	1.00	249.06	1	11.49	1.00	$\frac{1}{2773}$.00	$\frac{856}{2491}$.34
	79	54	F ^H	.21 ^W	.35	.01 ¹	1	4.00	.07	$\frac{6}{31}$.19	$\frac{4}{27}$.15
Ruellia humilis	79	54	S*	1.73 ^W	.81	.43	1	4.16	.45	$\frac{9}{122}$.07	$\frac{14}{112}$.13
	79	85	F ^H	22.01 ^W	1.00	62.44 ¹	1	4.00	1.00	$\frac{19}{33}$.58	$\frac{2}{36}$.06
	79	85	S*	2.44 ^W	.88	1.39	1	1.39	.60	$\frac{59}{72}$.82	$\frac{2}{4}$.50
	80	62	F	1.73 ^W	.81	1.14 ¹	1	4.00	.65	$\frac{1}{19}$.05	$\frac{4}{21}$.19
	80	62	S*	2.12 ^W	.85	6.25 ¹	1	2.00	.87	$\frac{3}{4}$.75	$\frac{4}{12}$.33
	79	64	F	1719.90	1.00	57.83 ^W	1	2.04	.98	$\frac{1}{1524}$.00	$\frac{1008}{1368}$.74
Rutibida columnifera													.00

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	Pr< χ^2	F value	V_1	V_2	Pr<F	Treatment (B)		Control (C)	
										actual fertil- potential ization	Percent fertil- ization	actual fertil- potential ization	Percent fertil- ization
Salvia pitcheri	79	129	F*	4.20	.96	2.45 ^{1W}	1	4.00	.81	$\frac{9}{184}$.05	$\frac{18}{168}$.11
	79	129	S	.02	.11	.66 ^{1W}	1	3.00	.52	$\frac{11}{36}$.31	$\frac{23}{72}$.32
	80	127	F*	190.30 ^W	1.00	2411.70	1	4.51	1.00	$\frac{1}{182}$.01	$\frac{126}{181}$.69
	80	127	S	.10 ^W	.25					$\frac{1}{4}$.25	$\frac{163}{504}$.32
Schrankia nuttallii	79	51	F	110.94	1.00	26.51 ^W	1	13.86	1.00	$\frac{0}{2597}$.00	$\frac{69}{1642}$.04
Senecio plattensis	79	42	F	153.93	1.00	4.24 ^W	1	3.01	.87	$\frac{2}{307}$.01	$\frac{102}{239}$.43
	80	35	F*	.42	.48	3.50 ^W	1	3.31	.85	$\frac{9}{207}$.04	$\frac{7}{222}$.03 ^E
Silphium integrifolium	80	107	F	100.67	1.00	22.52 ^W	1	4.00	.99	$\frac{11}{127}$.09	$\frac{88}{125}$.70
Solanum carolinense	79	77	F	5.76 ^W	.98	12.90 ¹	1	4.00	.98	$\frac{0}{19}$.00	$\frac{5}{19}$.26

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	Pr χ^2	F value	V_1	V_2	Pr<F	Treatment (B)		Control (C)		% B % C
										Percent actual fertili- zation	Percent potential fertili- zation	Percent actual fertili- zation	Percent potential fertili- zation	
<i>Solidago canadensis</i>	80	155	F	159.07 ^g	1.00	3.11	1	5.00	.86	$\frac{1}{445}$.00	$\frac{185}{615}$.30	.00
<i>Teucrium canadense</i>	80	84	F	2.00 ^g	.84	.89	1	.89	.47	$\frac{0}{54}$.00	$\frac{2}{55}$.04	.00
<i>Tradescantia bracteata</i>	79	38	F*	31.55	1.00	45.80 ^{1g}	1	4.00	.90	$\frac{14}{59}$.24	$\frac{42}{55}$.76	.31
	80	41	F*	9.33 ^g	1.00	2.72 ¹	1	4.00	.83	$\frac{1}{40}$.03	$\frac{8}{29}$.28	.09
	80	41	S	.17 ^g	.32	.13 ¹	1	1.00	.22	$\frac{1}{3}$.33	$\frac{11}{24}$.46	.73
<i>Tragia betonicifolia</i>	80	164	F	.80 ^g	.63	.01	1	5.76	.08	$\frac{1}{45}$.02	$\frac{3}{51}$.06 ^E	.38
<i>Triodanis perfoliata</i>	79	65	F*						.00 ^W	$\frac{2}{3}$	1.00	$\frac{4}{4}$	1.00	1.00
	79	65	S	256.62	1.00	5.87 ^{1g}	1	4.00		$\frac{383}{519}$.74	$\frac{125}{519}$.24	3.06

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	$\text{Pr} \chi^2$	F value	V_1	V_2	Pr < F	Treatment (B)		Control (C)	
										actual potential	Percent fertil- ization	actual potential	Percent fertil- ization
Verbena bipinnatifida	79	76	F*	77.43	1.00	22.54 ^W	1	4.05	.99	$\frac{21}{142}$.15	$\frac{80}{117}$.68
	79	76	S	304.87 ^W	1.00					$\frac{70}{568}$.12	$\frac{302}{468}$.65
	80	135	F*	6.60	.99	2.01 ^W	1	4.06	.77	$\frac{102}{180}$.57	$\frac{15}{43}$	1.62
	80	135	S	11.75 ^W	1.00					$\frac{292}{408}$.72	$\frac{42}{44}$.95
	80	159	F*	54.91 ^W	1.00					$\frac{3}{99}$.03	$\frac{13}{20}$.75
	80	159	S	2.71 ^W	.90	.08	1	.83	.17	$\frac{8}{12}$.67	$\frac{45}{52}$.05
	80	107	F*	437.23	1.00	23.37 ^W	1	4.14	.99	$\frac{161}{554}$.29	$\frac{592}{677}$.77
	80	107	S	229.34 ^W	1.00					$\frac{392}{644}$.61	$\frac{2061}{2368}$.33
Verbena hastata	80	112	F*	513.25	1.00	52.51 ^W	1	4.00	1.00	$\frac{155}{512}$.30	$\frac{700}{768}$.70
	80	112	S	192.34 ^W	1.00					$\frac{408}{620}$.66	$\frac{2472}{2800}$.33
													.75

Table 2 continued

Species	Year	Day Average	Fruit or Seed	χ^2	Pr χ^2	F value	V_1	V_2	Pr χ^2	Treatment (B)		Control (C)	
										actual fertil- potential	Percent fertil- ization	actual fertil- potential	Percent fertil- ization
Verbena stricta	80	94	F*	47.56	1.00	4.95 ^W	1	4.29	.91	120 441	.27	217 435	.50
	80	94	S	.00 ^W	.00					417 480	.87	754 868	1.00
Vernonia baldwini	80	101	F	378.38 ^W	1.00	630.80	1	3.16	1.00	17 642	.03	229 425	.54
	80	125	F	265.78 ^W	1.00	402.88	1	1.86	1.00	0 386	.00	135 249	.54

^W Best test to analyze this particular data

1 Analysed with 1 way ANOVA without subsampling

+ Data not used

* Type of data (either fruit or seed) used for the plant species unit

W Wilcoxin's Rank Sum Test used

A Low fruit set due to intricate pollination system

B Low sample size due to cage disturbance

C % B higher than % C due to low sample size

D Low sample size due to high flower/fruit predation

E Low fruit set due to drought

F Low sample size due to species rarity

G % B higher than % C because all C denominators extrapolated

H % B higher than % C due to high flower/fruit predation

distribution for the data could not be assumed. Therefore, the χ^2 statistic was deemed the most useful indicator of treatment differences. A T in Table 2 indicates whether the χ^2 or the F statistic is the most useful test to analyze each species unit data. A left-tailed probability was also determined for each χ^2 value. Rejection for H at the 0.05 level was 3.841.

Self-incompatible plant species -- From Table 2, plant species units that are largely self-incompatible were identified in one of 2 ways: (1) if the important statistic was \geq the value for rejection at the 0.05 level, or (2) a species unit was considered self-incompatible if it had $0 \leq \%B/\%C < 0.1$ since this indicated that only a very small percentage of the plants which had pollinators excluded from them were pollinated. This second method of identifying highly incompatible species only included those which had small sample sizes due to species rarity or overall low fruit/seed set. Thus their F or χ^2 values were not high enough for rejection under the first method of identification.

Weather correlations -- Spearman rank order correlations were used to correlate $\%B/\%C$ (= autogamy index) for species unit data with weather^{species}. It was also used to correlate averages of species unit data for time periods with weather-time^{species} and weather-time^{averaged}.

RESULTS

Autogamy in the Forb Community

Table 3 provides a summary of the importance of selfing in the tallgrass prairie forb community, with percent self-incompatibility being the results of the identification of self-incompatible species as enumerated in Methods. Another indicator of the amount of selfing in the community is the ratio of $\%B / \%C$ (autogamy index) for species units. This ratio is the best estimate of percent selfed progeny as compared to the overall reproductive success in a population at a certain time of the year under open pollination conditions. This is because $\%B$ represents only progeny produced by selfing and $\%C$ presumably represents progeny from both selfing and outcrossing. As taken from Table 2: 1) twenty-four of the 77 species units looked at produced at least 90% of their progeny by self-reproduction; 2) there was 46% reproductive success in $\%B$ as compared to $\%C$ for moderately to highly selfing species; 3) for the community as a whole, about 23% of the progeny were produced by $\%B$ as compared to $\%C$.

Both indicators of self-reproduction ($\%$ self-incompatibility and autogamy index) change throughout the growing season (Table 4). Yet, they show good correlation with each other (Figure 5). It is interesting to note that highly self-incompatible species were found throughout the entire growing seasons of both 1979 and 1980 ($\%B/\%C = 0$) even though the importance of self-reproduction reached some high levels for the community as a whole.

Table 3. The importance of self-reproduction to the forbs in the tallgrass prairie.

	<u>Species Units</u>			<u>Self-incompatible</u>		<u>Selfing¹</u>	
	<u>Self-incompatible</u>	<u>Selfing</u>	<u>Total</u>	<u>%</u>	<u>Mean %B/%C</u>	<u>%</u>	<u>Mean %B/%C</u>
1979	18	16	34	52.94	.069	47.06	.479
1980	28	15	43	65.12	.073	34.88	.446
Total	46	31	77	59.74	.072	40.26	.460

¹These are species units with a moderate to high degree of self-reproductive ability.

Table 4. The importance of self-reproduction within time periods.

Time period	Days ¹	Species Units		Autogamy Index (\$B/%C)	
		Self-incompatible/Observed	% Self-incompatible	Mean	Minimum Maximum
1979	2	22-43	5/5	100.00	.07 0 .31
	3	44-99	11/22	50.00	.54 0 1.64
	4	100-129	2/7	28.57	.61 0 1.31
1980	6	21-56	6/7	85.71	.15 0 .84
	7	57-104	8/13	61.54	.64 0 2.63
	8	105-120	6/10	60.00	.48 0 1.06
	9	121-140	3/6	50.00	.60 0 1.36
	10	141-174	5/7	71.43	.20 0 .83

¹Day 1 = April 29

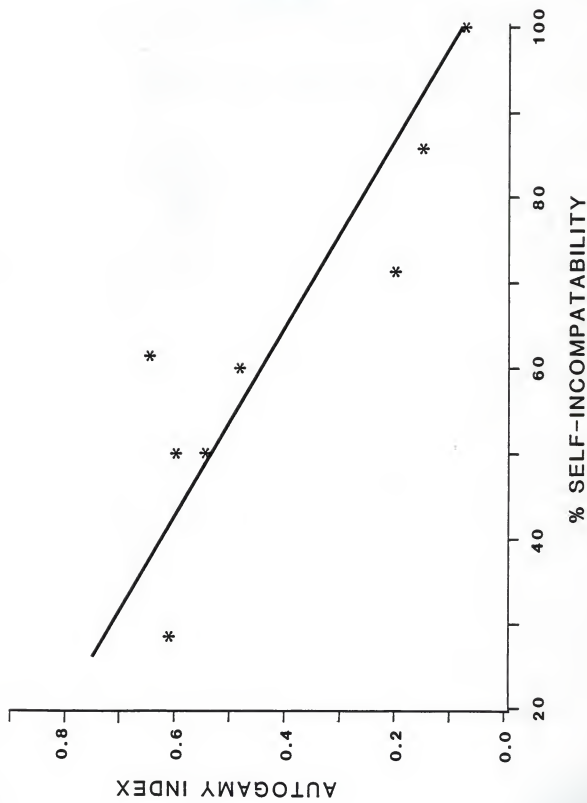


Figure 5. A comparison of two indicators of the extent of self-reproduction for time periods in 1979 and 1980.

Weather Correlations

As summarized in Table 5, when the autogamy index for species units was correlated with individual weather species indices, no significant correlation was found. The correlation of weather-time^{species} with the pollination ratio in time periods was also very low. However, the correlation of weather-time^{average} with the autogamy index for time periods is in the expected negative direction (Figure 6) ($r_s = -0.57$, Prob. = 0.14).

DISCUSSION

Selfing in the tallgrass prairie forb community

"Self-incompatibility is the rule" (Faegri and van der Pijl 1966). Indeed in many habitats, in terms of biomass contributions, plant species are overwhelmingly characterized by outcrossing (Moldenke 1976). Yet, if cross-pollination does not take place, self-fertilization is at least possible for many plant species. With the exception of those which are strongly self-incompatible, it can be assumed that a rather large proportion of the yearly seed output is the result of this kind of accidental autogamy (Faegri and van der Pijl 1966).

For the forbs in the tallgrass prairie, self-incompatibility is the rule by a narrow margin since 60% of the species were found to be self-incompatible. Self-reproduction produces 23% of the successful reproductive effort for all species. Even for highly self-incompatible

Table 5. Spearman rank correlations of autogamy index with weather indices. Weather species is correlated with $\%B/\%C$ for individual species units without regard to time period. Weather-time species and weather-time averaged are means of $\%B/\%C$ for species units as grouped into time periods.

Autogamy Index ($\%B/\%C$)	Weather species			Weather-time species			Weather-time averaged		
	N	r_s	Prob.	N	r_s	Prob.	N	r_s	Prob.
	77	-.05455	.6375	8	.07143	.8665	8	-.57143	.1390

r_s = Spearman rank correlation coefficient

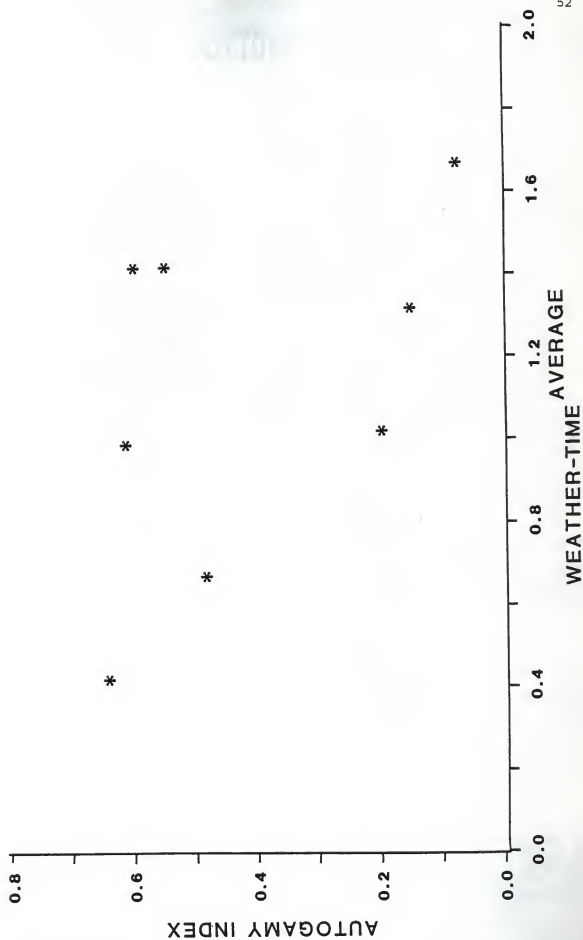


Figure 6. Data for correlating weather that affects pollinator activity with estimates of the extent of self-reproduction during time periods in 1979 and 1980 ($r_s = -0.57$). Weather-time^{average} is the best estimate of the long-term weather experienced by the forb community.

species, 7% of the progeny are from autogamous reproduction. Selfing seems to be a very important reproductive strategy for the tallgrass prairie community. Moldenke (1976) also found habitual selfing to be the most abundant strategy in grassland (41-43% of the species habitually selfed)) out of all the community types he examined in California.

In this study, the differences observed between percent selfing in 1979 and 1980 (Table 3) is largely due to the lack of data taken at the end of 1979. If this sample had been taken at the end of 1979, it presumably would have had a higher number of self-incompatible species than the yearly average indicated.

Correlations with weather data.

Optimally, the pattern of selfing through a growing season should be correlated with direct measurements of pollinator flight activity. A number of problems exist for collecting this type of data on a community-wide scale, however: 1) What quantity of insects constitutes an adequate statistical sample; 2) how do we define true pollinators; 3) a schedule for observing plants to note diurnal variations in pollinators; and 4) phenological variations in pollinators on plant species cause pollinating insect species to have various degrees of importance through the growing season. Hence, weather factors that presumably influence pollinator activity were used to predict periods where selfing would be advantageous.

Some problems are also inherent in the collection and use of weather data. For one, measurements of weather variables were not taken on the prairie. Also, as stated before, our understanding of the

effects of weather on pollinator activity in natural communities is virtually non-existent. Weather and other factors such as nesting materials and sites, shelters, parasites, food supply at emergence, overwinter conditions, predators, diseases, and fungi all play a part in pollinator population sizes which would directly affect pollinator activity (Lundie 1925, Vansell 1942, Peck and Bolton 1946, Linsley and MacSwain 1947, Bohart 1952, Hobbs and Lilly 1954, Stephen 1955, Holm 1966, Bohart 1967). In fact, pollinator population sizes are sure to vary through the growing season (Robertson 1895, Wood 1965). Yet, measurements that influence insect populations were not considered in the analysis nor does it seem possible that these could even be enumerated.

In the summer of 1980, there was a period of unseasonably hot and dry weather at the study site. Many species did not even flower during this summer (see Figure 7). This drought caused several anomalies in the data. Plants can only fill a certain number of fruits or seeds for energetic reasons. Consequently, during this time of stress, some plants had low %B and %C which could be attributed to either energetic constraints for the plants or the absence of pollen vectors for a largely self-incompatible species. Yet because the two treatments appeared the same, the F-test and high autogamy indices indicated self-compatibility when in reality this was not the case. Some data could not be used due to this erroneous conclusion (e.g., Senecio plattensis). Even when this was not the case, abnormally high autogamy indices caused some noise in the overall data set (e.g., Salvia pitcheri, Dalea candida, Tragia betonicifolia).

By grouping daily weighted weather scores into time periods

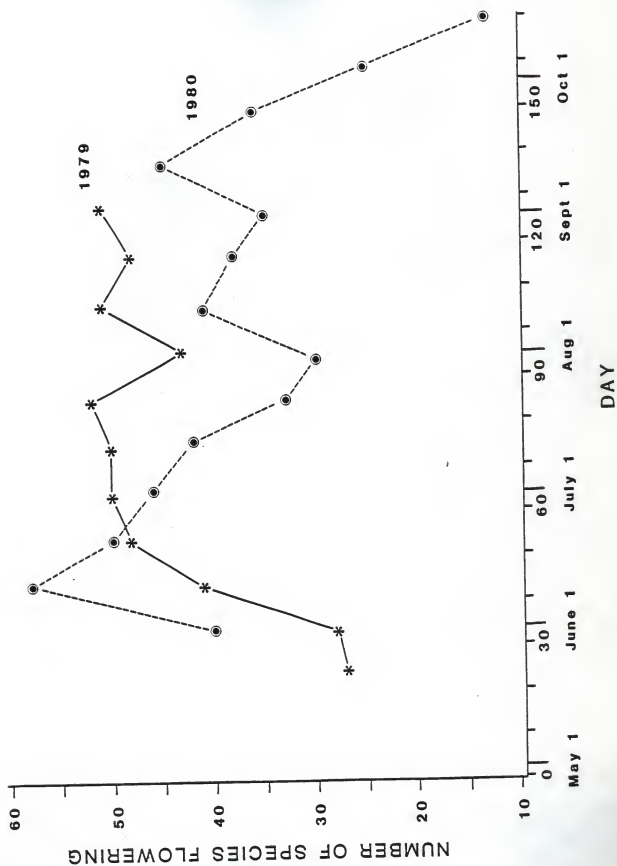


Figure 7. Number of species found flowering during census periods in 1979 and 1980. Note that there was no significant rainfall between days 53 and 83 during 1980. Day 1 is April 29.

according to how these scores changed and pooling plant species within these time periods, as much effort as possible was made to bias the autogamy data for correlation with weather-timespecies. Thus, if a trend was not seen, then it would either be due to the plant species cuing on long term weather patterns or that there was no correlation between amount of selfing in the forb community and pollinator activity as influenced by weather. Since indeed no significant correlation was found either with species grouped into time periods or as individual species units, it can be presumed the one of the latter two situations exists.

Weather-time^{average} is the best representative of weather that affects pollinators during a particular time of year. In the absence of many years of weather data, weather-time^{average} is the best index of the evolutionary experience of the forbs on the tallgrass prairie. Since there was a predicted negative correlation of weather-time^{average} with the index for selfing in time periods, validity is given to the idea that forbs in the tallgrass prairie may, to some extent, have their reproductive strategies adapted to long-term weather factors that influence pollinators.

Selfing reproductive strategy in response to
long-term environmental patterns.

Grasslands are characterized by extremes in weather: drought, blizzards, cloudbursts, tornados, bitter cold, and intense heat. There is little biotic buffering of environmental fluctuations like those that occur in the forest (Weins 1974). The relative variability of rainfall is high on the grassland; wet or dry years which differ by 1/4 of the

mean occur in 1 out of 4 years (Weins 1974). Furthermore, a dry year not only has low precipitation, but is accompanied by higher-than-average temperature and wind movements (Borchert 1950, Trewartha 1961, Weins 1974). Overall, the weather undergoes strong seasonal shifts and yearly differences.

These unpredictable periods of large variations in weather are fairly recurrent from year to year. For example, roughly $3/4$ of the yearly rainfall in the Great Plains grasslands consistently falls in the summer. This is due to wet and dry periods alternating every 5-7 months (Weins 1974). With weather on the tallgrass prairie being so extreme yet predictably seasonal, it would be advantageous for the forbs to reproduce autogamously during the times when weather has a detrimental effect on pollinator activity. Presumably, these breeding responses could become genetically fixed and coincide with long-term environmental patterns.

Weather-time^{average} is the best representative of this long-term pattern. Extremely wet or dry years (which differ by at least $1/2$ the mean), such as was experienced in this study during the summer of 1980, only occur every 1 in 42 years (Weins 1974). Hence, weather data collected during 1980 is fairly atypical. An average of many years of weather data would be a better representative of seasonal weather that affects pollinators. Presumably, this would correlate better with the autogamy index.

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APPENDIX 1

List of all plant species treated in the study. A '*' before the name indicates that the species was treated twice during that time period.

Time period 2 (1979):

Erigeron annuus (L.) Pers.

Oxalis violacea L.

Rosa arkansana Porter var. suffulta (Greene) Cockerell

Senecio plattensis Nutt.

Tradescantia bracteata Small

Time period 3 (1979):

Achillea millefolium L.

Amorpha canescens Pursh.

Cacalia plantaginea (Raf.) Shinnery

* Callirhoe involucrata (T. & G.) A. Gray

Calylophus serrulatus (Nutt.) Raven

Croton monanthogynus Michx.

Dalea candida Michx. ex Willd. var. candida

Hieracium longipilum Torr.

Linum sulcatum Riddell

Lythrum alatum Pursh.

Oenothera macrocarpa Nutt. subsp. macrocarpa

Opuntia macrorhiza Engelm. var. macrorhiza

Physalis virginiana Mill.

Polygala verticillata L.

* Ruellia humilis Nutt.

Rutibida columnifera (Nutt.) Wooten & Standley

Schrankia nuttallii (DC.) Standl.

Solanum carolinense L.

Triodanis perfoliata (L.) Nieuwl

Verbena bipinnatifida Nutt.

Time period 4 (1979):

Croton capitatus Michx.

Euphorbia marginata Pursh.

Gaura parviflora Dougl.

Lespedeza violacea (L.) Pers.

Physalis virginiana Mill.

Polygala verticillata L.

Salvia pitcheri Torr.

Time period 6 (1980):

Asclepias viridis Walt.

Baptisia bracteata var. glabrescens (Larisey) Isely

Callirhoe alcaeoides (Michx.) A. Gray

Erigeron strigosus Muhl.

Hymenopappus scabiosaeus L'Herit

Rorippa sinuata (Nutt.) Hitch.

Tradescantia bracteata Small

Time period 7 (1980):

Cacalia plantaginea (Raf.) Shinnery
Croton capitatus Michx.
Dalea purpurea Vent. var. purpurea
Desmanthus illinoensis (Michx.) MacM.
Gaura parviflora Dougl.
Hedvotis nigricans (Lam.) Fosb.
Lactuca ludoviciana (Nutt.) Riddell
Lythrum alatum Pursh.
Physalis virginiana Mill.
Ruellia humilis Nutt.
Teucrium canadense L. var. occidentale (Gray)
Verbena stricta Vent.
Vernonia baldwini Torr. var. interior (Small) Schubert

Time period 8 (1980):

Croton capitatus Michx.
Croton monanthogynus Michx.
Hieracium longipilum Torr.
Hedvotis nigricans (Lam.) Fosb.
Kuhnia eupatorioides L. var. corymbulosa T. & G.
Lactuca ludoviciana (Nutt.) Riddell
Physalis virginiana Mill.
Silphium integrifolium var. laeve T. & G.
 * Verbena hastata L.

Time period 9 (1980):

Ambrosia artemisiifolia L.

Cirsium altissimum (L.) Spreng.

Hieracium longipilum Torr.

Kuhnia eupatorioides L. var. corymbulosa T. & G.

Salvia pitcheri Torr.

Verbena bipinnatifida Nutt.

Vernonia baldwini Torr. var. interior (Small) Schubert

Time period 10 (1980):

Allium stellatum Ker.

Aster ericoides L.

* Cirsium altissimum (L.) Spreng.

Solidago canadensis L.

Tragia betonicifolia Nutt.

Verbena bipinnatifida Nutt.

AUTOGAMY AS A FERTILITY ASSURANCE STRATEGY
FOR FORBS IN THE TALLGRASS PRAIRIE

by

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ABSTRACT

Inbreeding is very important to the forbs of the tallgrass prairie. In fact, 40% of the prairie species were found to be moderately to highly self-compatible, 24 of the 77 species units (species treated at a given time) studied produced at least 90% of their progeny by self-reproduction, and 23% of the successful reproductive effort for all species was by autogamous means. It has been hypothesized that within a community some species may find it advantageous to become less reliant upon outcrossing as the probability for pollinator effectiveness decreases. Instead, they shift more toward inbreeding as a fertility assurance mechanism. In testing this hypothesis, each day in the 1979 and 1980 growing seasons was given a weighted measure of the probability for pollinator effectiveness based on 11 weather factors. These weighted measures were then grouped into time periods and field measures were taken to estimate the amount of autogamy during these time periods. No significant correlation was found between the probability for pollinator effectiveness and the estimates of the degree of autogamy. This indicates that the forb community as a whole shows little facultative ecological response in its type of breeding. However, the weather index that represented the evolutionary experience of the plants showed a predicted negative correlation with self-reproduction in time periods. This lends support to the hypothesis that the reproductive strategies of forbs in the tallgrass prairie are adapted to long-term weather factors that influence pollinators.